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THE CASE OF THE BLUE ANDALUSIAN¹

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THE blue Andalusian has become the classic in animals as an example of a heterozygote phenotypically intermediate between the parental types. It has also served as an illustration of the failure of dominance for those opponents of Mendelism who consider dominance one of its fundamentals. Furthermore, it has been in constant demand as a classroom example of blended inheritance.

The main facts concerning the breeding behavior of blue Andalusians are, accordingly, more or less familiar. In spite of the long-continued efforts of their breeders they do not come true to color as a breed, but continually throw a certain proportion of off-colored progeny, or "wasters," of two kinds. One is self (entirely) black. The other approaches white, but displays considerable pigment, and is referred to variously as white, splashed, and splashed-white. Since an examination of a large number of birds of this type shows the pigmented feathers to be *blue* in all sections of the female and in those sections of the male which carry blue feathers in the blue Andalusian male, they will be referred to throughout this paper as blue-splashed.

"Splashed" refers to the fact that the pigment does not regularly appear in any particular group of feathers or in any definite region. Feathers located apparently at random on any part of the body may be pigmented over their entire surface or may show only slight traces of pigment. Not infrequently both of these conditions are present in the same individual.

Since the blacks and blue-splashed breed true when

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mated *inter se*, they are considered as being homozygous. If crossed they invariably produce blues.

These facts have led to the current view that the case involves a single allelomorphic pair of characters. The blacks and blue-splashed represent the homozygous conditions, while the self blue is the heterozygote between the two. When blues are interbred, blacks, blues, and blue-splashed are produced in a ratio approximating 1:2:1 for these classes, respectively, which seems to corroborate this view.

Although the blacks and blue-splashed breed true for color, they are not recognized by fanciers as 'breeds or varieties, and it is doubtful whether they would continue to exist if, much to the disgust of the breeders of blue Andalusians, they did not continue to appear as "wasters" among the progeny of blues. The blues, on the other hand, are quite widely bred. They are officially recognized by the American Poultry Association as a distinct breed and have their place in the American Standard of Perfection. It is interesting in this connection to note that the numbers of blues they throw on the Mendelian expectation barely gets them into the Standard, since the rules of the Association are that no breed can be officially recognized as such unless a minimum of 50 per cent. of the offspring come reasonably true to type (American Poultry Association, 1910, p. 328, Constitution, Article XI).

The blues are quite uniformly bluish-gray throughout the body, with certain exceptions in the males to be noted later. Emphasis has usually been laid on their distinctness from the black and the blue-splashed birds, but it seems important to note their resemblance to these two classes. In the first place, they are like the blacks in being *self-colored*, that is, all feathers in all parts of the body are pigmented. In the second they resemble the blue-splashed in that the color of the individual pigmented feathers is *blue* rather than black, save in certain sections of the males of both classes, where the feathers showing

pigment are a glossy black, apparently a secondary sexual characteristic. The blue appearance is due to the distribution and arrangement of the pigment granules in the feather structure, as will be described later. The fact that the splashed birds are splashed with blue (with the exception noted above) rather than black is important and appears not to have been noted, or at least not emphasized, by previous writers.

As an example, Punnett (1911, p. 70), in discussing the breeding behavior of the blue Andalusian, says: "It always throws 'wasters' of two kinds, viz., blacks, and whites *splashed with black*" (*italics mine*). In the material which has come under my observation, consisting of upwards of one hundred birds in the unrelated flocks of the poultry departments of Kansas State Agricultural College and the University of Wisconsin, no individual has been noted in which the pigmented areas were not distinctly bluish-gray, except that those pigmented feathers or parts of feathers appearing in the hackle, back, and saddle of the male were glossy black. These sections, it should be clearly understood, are also glossy black in the blue Andalusian male. There are occasionally flecks or small spots of black, appearing in the blue-gray feathers, and even in the white feathers of the blue-splashed birds. This is also true of the blues and, indeed, is not a rare occurrence in both dominant and recessive white races of other breeds. It does not in the least affect the fact that, in the material so far observed, the white birds have been splashed with bluish-gray rather than black in those sections where the blue Andalusian is also blue. This conclusion is borne out by the results of a microscopic examination.

In an effort to determine the fundamental differences between the three Andalusian phenotypes, a careful study of feathers from numerous individuals of each phenotype was made. A detailed account of the results of the study will be published in a later paper. For present purposes a short account of the most obvious differences will serve.

The pigment in all three phenotypes is black. The differences in appearance are due to the distribution and arrangement of the pigment or to its absence.

The pigment in a black Andalusian feather is in the form of rod-shaped granules, which almost completely fill each cell. They extend to the very tips of both curved and hooked barbules, and into the tiny hooklets given off from the barbs of the latter class. The cell boundaries are usually visible, due, apparently, to a slight contraction of the pigment, leaving very narrow pigment-free spaces between the cells. The former position of the nucleus of each cell is almost always plainly visible, due to an accumulation of pigment at its border, and to a narrow area surrounding it that bears relatively little pigment. In appearance, size and distribution the pigment granules in feathers from the black Langshan seem to be identical with those of black Andalusians.

The feathers from blue Andalusians differ from those of the blacks in two important particulars, namely, the restriction of the pigment in the feather structure and the shape of the granules. In blues of average shade, pigment fails to appear in the extremities of the barbules of both types. The hooklets are also entirely pigment-free. Though not always the case, the curved barbules usually carry rather more pigment than the hooked barbules, since the pigment extends further toward the distal end. As a usual thing that part of the hooked barbule which bears the hooks is free from pigment and does not differ in appearance, by transmitted light, from the same portion of a similar barbule from a white feather.

In the pigmented portions the pigment is usually markedly contracted or clumped within each cell, leaving a pigmentless space about the border much wider than is the case with blacks. These spaces are not always clean cut, but may be broken by invading rows of granules, or isolated granules may be found scattered within them. As a usual thing the nuclear boundaries in the cells of blue-gray feathers can only be made out with difficulty, if at all.

In cross-section, the pigment granules are seen to be scattered through the cortex of the barb and along the boundaries of the medullary cells. They are not restricted to the apex of the barb, as is reported by Lloyd-Jones (1915, p. 472, Figs. 37-39) in the so-called blue pigeon.

The predominating shape of the pigment granules in feathers from blue Andalusians is round. There may be a few elliptical granules and occasionally one which can not be classified otherwise than as a rod. These are quite rare, however, and one may carefully scrutinize several blue-gray feathers without finding any but round or very slightly elliptical granules. These round granules quite frequently appear in straight rows, giving the effect of a string of beads.

While the granule shape may have an appreciable effect in giving the bluish-gray cast found in blues and blue-splashed, it seems more likely that, as suggested above, the bluish appearance is due to the restriction or arrangement of the pigment. While the condition is not precisely the same as in pigeons, as described by Cole (1914, pp. 324-325) and Lloyd-Jones (1915, pp. 472-473), the optical effect appears to be from essentially the same causes, namely, the clumping of the pigment within the cells, and the reflection from this pigment through more or less transparent layers of keratin. It appears, however, that in the blue Andalusian the contrast between the pigment-free ends of the barbules and the pigmented barbs and barbule-bases is of more importance in producing the bluish effect than is suggested for the pigeon by these writers.

A characteristic of the typical blue Andalusian not before mentioned is that the contour feathers on the female and the breast feathers on the male present a laced appearance. This results from a black edging on that portion of each feather which is exposed when in its natural position. In this part of the feather the barbules on both sides of the barb are alike, being without hooks. The

cells in these barbules are more heavily pigmented than is true of the rest of the feather and the granules are rod shaped. In the regions where the black is giving way to blue, both round and rod-shaped granules are found.

All pigmented feathers secured from several blue-splashed females show identically the same pigment arrangement and granule shape as predominates in the blues. This holds true whether the portion examined comes from a feather that is pigmented throughout, or from one that is almost wholly white, with but a trace of pigment showing. In feathers which are pigmented throughout, the same relation regarding the lacing occurs as in homologous feathers in blue females.

The statements of the foregoing paragraph apply equally well to the feathers of those sections of the blue-splashed male which are blue in the blue male.

As previously mentioned, in both blue-splashed and blues, as well as in other self-colored races, black flecking or spotting not infrequently appears. Such spots, whether taken from a blue feather from a blue individual, or from a blue or an almost white feather from a blue-splashed bird, invariably show rod-shaped granules, while the surrounding area, if blue-gray, shows round granules. These spots are apparently entirely independent of the factors and conditions discussed in this paper and their appearance is comparatively limited. If hereditary, they probably depend on other factors. In handling blues and blue-splashed, however, one can not help being impressed with the possibility that these spots are caused by some interference with the full expression of the factors responsible for the arrangement and rounding of the pigment granules. Whether this interference is hereditary or environmental is as yet undetermined.

One further fact concerning the blue Andalusian males, already alluded to, is of interest. The long feathers of the neck (hackle) and saddle are glossy black. This is apparently a secondary sexual characteristic, though it is as yet undetermined whether it is due to the presence of

testicular secretion or the absence of ovarian secretion. The black feathers from both sections show rod-shaped granules predominating. There are numerous elliptical granules and a few round granules present. The pigment is not restricted as to distribution in the feather structure and is found even in the tiny hooklets of the hooked barbules, being in all these respects similar to the analogous feathers on a black male. These same conditions prevail in homologous pigmented feathers in a blue-splashed male.

The foregoing describes the conditions that usually prevail. There is some variation in all conditions described. In pure-bred blue Andalusians, for instance, there frequently appear areas that are not the usual clear blue-gray, but are dull and smoky. In such regions both round and rod-shaped granules are found in about equal numbers.

Bateson and Punnett (1906, p. 20) make note of the fact that the adult color of Andalusians may be determined from the down color of the young chicks. Examinations of the down show the same differences in granule shape that are observed in the adults. The blue and blue-splashed chicks for the most part show nothing but round granules in the down, while the blacks show rods.

It is of interest to note in this connection that a section from that portion of a barred Plymouth Rock feather where the black bar is giving way to the white, and the color is dull gray or dun with no bluish cast, there is a dilution of pigment as to amount, but no restriction as to arrangement or distribution. The pigment is fully extended through the barbule cells and consists of rod-shaped granules. There simply appears to be less pigment. While this is the usual condition, here, too, there is variation. At least one barred Rock individual was found whose feathers showed numerous round granules, though the rods predominated.

While it is generally accepted that blue Andalusians, when mated *inter se*, produce blacks, blues and blue-splashed in the ratio of 1 black to 2 blues to 1 blue-

splashed, exact data on this mating, as well as on the back crosses to black and blue-splashed, are really very meager. Bateson and Saunders (1902, p. 131) first suggested that the blue Andalusian was probably a heterozygote. Bateson and Punnett (1905, p. 118) quoted Mrs. Blacket Gill, a fancier of blue Andalusians, to the effect that blues mated to blues gave 22 blacks, 36 blues and 17 white-splashed (*i. e.*, blue-splashed). They secured stock from Mrs. Gill and made matings which gave the following results:

By the blue ♂ the white ♀ gave 34 blue, 20 white-splashed, and the black ♀ gave 27 blue, 19 black. In each case the result is qualitatively what would be expected if the blue is a heterozygote of *black* × *splashed white* [*italics mine*]; but whether the departure from equality indicates that some gametes bear the unsegregated blue, or may merely be taken as individual irregularities, can not yet be stated.

The same blue cock was bred with a black hen from Experiment 40 (in which the dark birds were unexpected), F₂, from White Wyandotte × Wh. Legh., giving as offspring 10 black, 15 slaty black to bluish. Hence, therefore, it is evident that the black ♀ was a homozygous black. The 10 blacks are the result of the union of the black gametes from the Andalusian ♂ with those of the ♀, and the 15 slaty resulted from the meeting of the black of the hen with the white-splashed from the Andalusian.

Bateson and Punnett (1906, p. 20) give the following summary of the data upon which the case of the blue Andalusian largely rests at the present time.

In Report I it was suggested that the blue colour of the Andalusian is probably heterozygous, and in Report II (p. 118) figures were given in support of this view. During the past two years additional evidence has been acquired, and every form of mating has now been tested, with the following results:

No. of Experiment	Nature of Mating	Result		
		Black	Blue	Wh. Spl.
Rep. II, p. 118.....	Blue ♀'s × blue ♂'.....	22	36	17
Exp. 276.....	Blue ♀'s × blue ♂'.....	19	42	22
(Total numbers for blue and blue.....		41	78	39)
[Expectation (inserted by the writer).....		39.5	79	39.5]
Rep. II, p. 118.....	Wh. spl. ♀ × blue ♂'.....	—	34	20
" " ".....	Black ♀ × blue ♂'.....	19	27	—
Exp. 269.....	Wh. spl. ♀'s × wh. spl. ♂'.....	—	—	40
" 270.....	Black ♀ × wh. spl. ♂'.....	—	20	—
" 294.....	Black ♀ × black ♂'.....	25	—	—

The colour of most of the chickens was determined in the down. In the blacks the down is black with the exception of the ventral surface, the tips of the wings, and sometimes parts of the head, which are white. The down in the blues is slaty-blue, similarly marked with white, whilst in the white splashed it is of an exceedingly pale blue tint as a rule, though sometimes practically colourless.

The above figures bear out the view we previously expressed as to the heterozygous nature of the blues, . . .

The only other definite figures that have come under the writer's notice are from W. J. Coates, a blue Andalusian breeder of East Calais, Vermont, quoted by Platt (1916, p. 665) and referred to by Pearl (1917, p. 149). These are for matings of blue to blue and are as follows:

Mating	White (Blue-Splashed)	Blue	Black	Dark Red
A.....	4	10	3	1
B.....	4	5	2	0
C.....	3	3	0	3
D.....	0	12	1	0
E.....	3	3	1	0
	14	33	7	4

The fact that birds showing dark red appear is unusual and would seem to indicate that the Coates stock differs in its genetic constitution from the majority of the members of the breed, unless the occasional appearance of red is a fact usually suppressed by breeders.

Bateson and his co-workers make no attempt beyond that quoted above to account for the hereditary behavior of Andalusians and appear content to rest the case on the assumption that "blue is a heterozygote of black \times splashed white."

The fact that "blue" is not a true intermediate between black and blue-splashed does not seem to have received due consideration. While the blue-gray bird is in a sense intermediate between self black and an individual that approaches white more or less closely, this intermediacy is more apparent than real. As previously pointed out, it is not intermediate in regard to either of the conditions involved when they are considered sepa-

ately. It resembles the black phenotype in being self-colored and the blue-splashed phenotype in having the pigment restriction within the barbules, which gives the blue-gray effect.

The 1:2:1 ratio may therefore be analyzed as follows:

Phenotypes	<div> <div> Pigment <i>not re-</i> <i>stricted</i> in bar- bule cells; <i>ex-</i> <i>tended</i> through plumage ("self" condition); phe- notype black. </div> <div> Pigment <i>re-</i> <i>stricted</i> in bar- bule cells; <i>ex-</i> <i>tended</i> through plumage (self); phenotype blue. </div> <div> Pigment <i>re-</i> <i>stricted</i> in bar- bule cells; <i>not ex-</i> <i>tended</i> through plumage; pheno- type blue- splashed. </div> </div>		
Ratio of pheno- types	1	:	2 : 1
Ratio for restric- tion in barbules	1	:	3
Ratio for exten- sion in plum- age	3	:	1

In reality, then, the 1:2:1 ratio is the result of the combination of two 3:1 ratios.

The foregoing facts appear to lend themselves equally well to two interpretations. The first is that there are two pairs of allelomorphic factors at work. The second, that there is one pair of true allelomorphs (*i. e.*, factors having identical loci on homologous chromosomes), neither of which is recessive to the other in its manifestation in the phenotype.

The suggestion of two pairs of allelomorphic factors to explain the case of the Andalusian is not a new one. Goldschmidt (1913, p. 274) makes such a suggestion. After pointing out that the offspring of a pair of blues are black, blue, and "*schmutzigweiss*" in the ratio of 1:2:1, and that all three phenotypes carry pigment, he proposed two factors to account for the condition. The one is an "*Entfaltungsfaktor*," which brings about a full development of the pigment. He represents this factor by "*Q*" (*Quantität*) which is possessed by the black race. The other factor, which is possessed by the "*Weisse*" race, he calls a "*Mosaikfaktor*," which finely divides the pigment. This factor he designates *M* (*Mosaik*). He

finds it necessary to postulate further that Q is closely linked with m , and M is closely linked with q . Assuming pigment (P) to be present in all cases, he represents the "black" gamete as (mPQ), the "white" gamete as (MPq), and the F_1 blues as (mPQ)(MPq). The blue results from bringing M and Q into the same zygote. The monohybrid ratio results when the blues are inbred, however, because of the close coupling of the factors within the parentheses.

The Hagedoorns (1914, p. 179) also make use of two coupled factors in accounting for the hereditary behavior of blue Andalusians. They state:

A blue Andalusian fowl, when mated by us to "recessive" white hens did not produce as many blue as white chicks, as should result on the hypothesis, that the white Andalusian is a recessive white (blue and black Andalusians being heterozygotes and homozygotes for one single genetic factor), but exclusively blacks and blues in equal proportions.

To account for this result they propose a gene A which is present in black Andalusians, but absent in the "white" Andalusian. The blacks, conversely, lack a gene B which is present in the "whites."

This factor B , present in a pigmented fowl, actively "dilutes" the colour. It has no effect in the white Andalusians, because these, as they lack A , are *not pigmented* [italics mine]. We should therefore expect dilute black (blue) young from the cross black \times white, which, inter se, would give AB , Ab , aB and ab offspring. Now, there is no evidence that in *Andalusians* there are ever produced $aabb$ animals, or $AABB$. There seems to be a mutual repulsion between A and B , so that no AB or ab gametes are ever produced. In some varieties of fowls this repulsion does not seem to exist, as pure strains of blue chickens occur.

Unless their material differs from any that has come under my observation the Hagedoorns err in assuming that what is frequently termed "the white Andalusian" carries no pigment, and Goldschmidt's suggestion accords more closely with the facts. Further, if the "recessive" white to which they refer was an Andalusian, the production of equal numbers of blues and blacks from a blue \times white (blue-splashed) cross is difficult to understand. The expectation would be equal numbers of blue-splashed

and blues. If, as I suspect, the "recessive" white was a true recessive from another race, their results can only be interpreted by assuming that the "white" gametes as well as "black" gametes produced by the blue fowl carried a factor necessary for pigment production, which was lacking in the recessive whites.

If the latter is the case it accords with results I have obtained the past season. Among several matings made, preliminary to a further study of Andalusian blue, a white Wyandotte ♂ (*R* 840 from the University of Wisconsin flock) was mated with blue-splashed Andalusian ♀♀ *M* 409 and *M* 539 (also kindly furnished by the poultry department of the University of Wisconsin). From *M* 409 seven chicks were hatched, all of which were unmistakably bluish-gray. Six chicks which failed to hatch, but which did develop far enough for the color of the down to be determined, were also all blues. From *M* 539, brought in late in the season with the hope of increasing the numbers of chicks from this type of mating, three chicks were secured, which were again all bluish-gray. On the assumption that Wyandotte white is recessive (I am surprised to find no statement to this effect in the literature) these results would seem to indicate that a factor necessary for pigment formation as well as one causing the characteristic arrangement or restriction of the pigment found in blues, and both lacking in the Wyandotte, were furnished by the blue-splashed Andalusian. And further that a factor for the extension of this pigment to all feathers on the body was furnished by the Wyandotte. The blue offspring from this mating are assuredly not intermediates between a pure white parent and one that appears to be nearly white.

It is significant to note in this connection that the blue-gray offspring of the white Wyandotte × blue-splashed Andalusian cross show pigment granules that are predominately round. In some individuals they all appear to be round, while in others some rods may be made out. The down of black chicks, offspring of a blue Anda-

lusian ♂ and a white Plymouth Rock ♀, showed only rod-shaped granules. Feathers from a blue-gray individual, whose dam was a blue-splashed Andalusian and whose sire was a crossbred, the offspring of a Houdan ♂ \times single-combed white Leghorn ♀ cross, showed only round granules.

If, as Goldschmidt assumes, his factors mQ and Mq are so closely linked that they never separate, and behave only as a single pair of factors, it is simpler to assume that there is but one pair of factors. As already pointed out, however, the discontinuity in the gradations from blue-splashed to black is such as to lead one strongly to suspect that two pairs of factors are at work. This discontinuity is greatly emphasized in the case of the blue offspring from the white Wyandotte \times blue-splashed Andalusian cross. It is perhaps not impossible that a single pair of factors should bring about the result found in Andalusians, but it is so unusual as to make the assumption of two pairs of factors reasonable.

If this assumption is correct it must be further assumed, as Goldschmidt implies but does not state, that the black and splashed races each contribute a dominant and a recessive factor, and that in the blues we have the expression of both dominants, namely, the extension of pigment to all feathers, furnished by the black (or, in the Wyandotte cross noted above, by the white) parent, and the restriction of the pigment in the feather structure in such a way that the effect is bluish-gray, furnished by the blue-splashed parent. It is of interest in this connection to note that the blue condition produced by the restriction of the pigment in the barbule cells is recessive in pigeons (Cole, 1914, p. 325), while in Andalusians, on the above assumption, it is dominant.

While exact data concerning the breeding behavior of blue Andalusians are exceedingly meager, the experience of breeders generally seems to be in accord with such data as there are, and with the interpretation offered by Bateson and his associates. In order to account for the fail-

ure to secure a dihybrid ratio from the mating of blues, one is driven to assume linkage, and apparently a quite close linkage, of the dominant of one allelomorphic pair to the recessive of the other. As I hope to make clear, however, the linkage may not be complete, since it would easily be possible for crossing-over to occur occasionally with very slight likelihood of detection.

Goodale (1917, p. 213) has very recently shown that crossing-over occurs in the sex chromosome of the male fowl, though he has not as yet presented his evidence in detail. The universality of the laws of heredity throughout the plant and animal kingdoms is such that it would be a matter of surprise if crossing-over in fowls did not also occur in chromosomes other than the sex chromosome.

There is at present no certain criterion by which to predict whether, having assumed crossing-over in the autosomes of fowls, it occurs in one sex only or in both; and if in but one sex, which it may be, unless one chooses to suppose that it occurs only in the sex homozygous for the sex chromosome, as in *Drosophila*. If it occurs in both sexes, it is apparently so rare an event in Andalusians that the probability of securing two cross-over individuals in a mating made for purposes of analysis is so small as to be almost negligible.

After a somewhat extended microscopic study of blue-gray feathers from blues, blue-splashed and certain crosses, it seems more in accordance with their apparent action to refer to the factor responsible for changing black into bluish-gray as a restrictor, designated as *R* rather than *M* (Mosaikfactor) as was done by Goldschmidt. Similarly in place of *Q* (Quantität) I would suggest *E*, as responsible for the extension of pigment to all the feathers of the body.

Using this terminology and assuming for the moment complete linkage, a cross between individuals of the black and blue-splashed races, respectively, would appear as follows:

$$\begin{array}{l} Er\ Er = \text{black} \times eR\ eR = \text{blue-splashed;} \\ F_1 \qquad \qquad \quad Er\ eR = \text{blue;} \end{array}$$

F_2 $1 Er Er = \text{black} + 2 Er eR = \text{blue} + 1 eR eR = \text{blue-splashed}$.

The gametes produced by the F_1 (blues) are Er and eR . If crossing-over should occur there would be occasional ER and er gametes produced. It is highly interesting to note that if these two classes of cross-over gametes were produced in equal numbers, as would be expected, and the individuals producing them were mated with ordinary blues, exactly the same phenotypic ratio would result as from the unions of the non-cross-over gametes, viz.:

F_1 crossover gametes
 ER, er

Ordinary gametes of F_1 blue
 Er, eR

F_2 $ER Er = \text{blue}, ER eR = \text{blue}, er Er = \text{black}, er eR = \text{blue-splashed}$.

This is the usual ratio of 1 black to 2 blues to 1 blue-splashed and would, from the very nature of the case, escape observation as involving crossing-over unless careful analysis were made of the hereditary constitution of these particular F_2 individuals.

Such analyses would not be impossible, though they might be long and tedious. The matings which would uncover any of the cross-over types, if offspring were produced in sufficient numbers to make it fairly certain that one were not dealing with chance variations in the ratios, are given herewith.

Cross-over blue of $ER Er$ constitution mated with an ordinary blue would give the following expectation:

$ER Er = \text{blue cross-over} \times Er eR = \text{ordinary blue};$

F_1 $ER Er = \text{blue},$
 $ER eR = \text{blue},$
 $Er Er = \text{black},$
 $Er eR = \text{blue},$

or 3 blues to 1 black, while the ordinary blues would give the normal 1 black to 2 blues to 1 blue-splashed.

Similarly this same individual mated with ordinary blue-splashed would produce all blues instead of the ordinary expectation of 1 blue to 1 blue-splashed, viz.:

$ER Er = \text{blue cross-over} \times eR eR = \text{ordinary splashed};$

F_1 $ER eR = \text{blue},$
 $Er eR = \text{blue}.$

If blue cross-over of the type $ER eR$ were mated with ordinary black the expectation would be all blues instead of the usual blues and blacks in equal numbers, viz.:

$ER eR = \text{blue cross-over} \times Er Er = \text{black};$

F_1 $ER Er = \text{blue},$
 $eR Er = \text{blue}.$

This second type of blue cross-over individual, $ER eR$, mated with ordinary blue, would give an expectation of 3 blues to 1 blue-splashed instead of the ordinary 1:2:1 ratio, viz.:

$ER eR = \text{blue cross-over} \times Er eR = \text{ordinary blue};$

F_1 $ER Er = \text{blue},$
 $ER eR = \text{blue},$
 $eR Er = \text{blue},$
 $eR eR = \text{blue-splashed}.$

If black cross-over $Er er$ were mated with ordinary blue the expectation would be 2 blacks to 1 blue to 1 blue-splashed instead of the ordinary ratio of equal numbers of blues and blacks, viz.:

$Er er = \text{black cross-over} \times Er eR = \text{ordinary blue};$

F_1 $Er Er = \text{black},$
 $Er eR = \text{blue},$
 $er Er = \text{black},$
 $er eR = \text{blue-splashed}.$

This same individual $Er er$ (black cross-over) mated with an ordinary splashed bird would give an expectation of half blues and half blue-splashed instead of all blues, as in the case of ordinary black and blue-splashed, viz.:

$Er er = \text{black cross-over} \times eR eR = \text{ordinary blue-splashed};$

F_1 $Er eR = \text{blue},$
 $er eR = \text{blue-splashed}.$

Finally, blue-splashed cross-over $eR\ er$ mated with ordinary blue would give an expectation of 1 black to 1 blue to 2 blue-splashed instead of the ordinary expectation of equal numbers of blues and blue-splashed, viz.:

$eR\ er$ = blue-splashed cross-over \times $Er\ eR$ = ordinary blue;

F_1 $eR\ Er$ = blue,
 $eR\ eR$ = blue-splashed,
 $er\ Er$ = black,
 $er\ eR$ = blue-splashed.

The possible matings not indicated in the foregoing are those which would produce the same phenotypic ratios as if ordinary individuals (*i. e.*, non-cross-overs) of the same appearance as the cross-overs were used. Such matings are naturally of no value for analysis.

If it should later be shown that crossing-over does occur as suggested above and there are two pairs of factors concerned, there is the possibility of occasionally securing ER gametes. This in turn would seem to make possible the blue Andalusian breeder's long-time dream of producing blues that "breed true." With the appearance of the double recessive gamete er another race of Andalusian would apparently become possible, which, if the factors assumed in this paper are correct, should be white splashed with *black* instead of with blue.

The second possible interpretation of the facts so far established is that my postulated factors R and E occupy identical loci on homologous chromosomes, neither being recessive to the other in its phenotypic expression. For the present at least any evidence that this is the correct interpretation will be largely negative and come from continued failure to find cross-over individuals with regard to R and E . If these cross-overs should not be found it might at first appear that the interpretation of the case of the blue Andalusian is in all probability exactly what has been suggested from the first, namely, that blue is a heterozygote intermediate between the parental types.

Such an interpretation makes the characters *black* and *blue-splashed* the allelomorphs.

The practise of referring to *characters* that seem to behave in an alternative relationship in heredity as allelomorphs, instead of *factors occupying identical loci on homologous chromosomes*, is, it is to be hoped, passing. That it has lead to a misinterpretation in the present case is shown by the fact that all the offspring of certain pure white birds mated with blue-splashed ones are blue. The *E* factor must have come from an individual that was homozygous for it and devoid of pigment. It appears reasonable to expect that among the F_2 's from the white Wyandotte \times blue-splashed Andalusian cross will appear pure whites that carry the *R* factor. If this proves to be the case the allelomorphs are two factors, *R* and *E*, which act on black pigment. *R* arranges and restricts the pigment in the feather structure so that it gives a bluish-gray appearance. *E* extends any black pigment present to all the feathers of the body. One and probably either or both may be present without any phenotypic expression whatsoever. In fact, for every sixteen F_2 individuals from this cross four pure whites are to be expected in which the genotypic ratio with regard to *R* and *E* is 1:2:1, exactly as in the F_2 's from a cross of a black and a blue-splashed Andalusian. One of these whites will be homozygous for *R* like the blue-splashed Andalusian. One will be homozygous for *E* like the black Andalusian. And two will be heterozygous for *E* and *R*, as are the blue Andalusians. But because there is no black pigment present these differences in the genotype do not affect the phenotype. For the sake of clearness the expectation of this cross is shown herewith, carried through the F_2 generation. *P* is taken to represent a factor necessary for the formation of pigment which is present in the blue-splashed Andalusian, but absent in the white Wyandotte, while *E* and *R* are represented as allelomorphic to each other.

White Wyandotte ♂ \times blue-splashed Andalusian ♀.

	<i>ppEE</i>	<i>PPRR</i>		
F ₁		<i>PpRE</i> = all blue;		
F ₂	6 blues:	3 blue-splashed:	3 black:	4 white.
	2 <i>PPRE</i>	1 <i>PPRR</i>	1 <i>PPEE</i>	1 <i>ppRR</i>
	4 <i>PpRE</i>	2 <i>PpRR</i>	2 <i>PpEE</i>	2 <i>ppRE</i>
				1 <i>ppEE</i>

This same ratio (6:3:3:4), which is to be expected on either interpretation, has been reported by Baur (1914, p. 95) for crosses between a white-flowered race and certain plants bearing ivory-colored flowers, of the snapdragon (*Antirrhinum majus*).

Recessive mutations are of comparatively frequent occurrence. Dominant mutations, though much less frequent, have been described so often that they can not be reasonably doubted. There appears to be no reason, *a priori*, why a mutation might not occur where the mutated factors' potency of expression in the phenotype is approximately equal to that of the normal factor. That this has occurred, not once, but several times, might be the interpretation placed on the striking allelomorphic series reported by Nabours (1914, p. 141) for the color patterns of the grouse locust (*Paratettix*).

Upon which of the two alternative interpretations is correct appears to depend the possible success or the futility of the search for true breeding blues. The first makes it possible. The second appears to close the door of hope in the Andalusian breeder's face unless hope is seen in the progressive selection of the darker blue-splashed individuals. It does not appear possible, on the basis of present known facts, to reach a conclusion. Extensive matings are being made for the coming breeding season which it is hoped will throw further light on the matter.

SUMMARY

1. This paper shows that blue Andalusians are like black Andalusians in that they are self-colored. They

are like the blue-splashed in that homologous pigmented feathers in both sexes have the same condition with reference to the restriction of pigment in the feather structure.

2. The fundamental phenotypic differences between black, blue and blue-splashed Andalusians are briefly described.

3. It is pointed out that the 1:2:1 ratio is in reality a combination of two 3:1 ratios.

4. The condition in the blues is shown to be due to the combined action of two factors *R* and *E*. *R* acts on black pigment, restricting its distribution in such a way that it gives the characteristic blue-gray appearance. *E* extends black pigment to every feather on the fowl's body.

5. It is impossible to decide on the basis of present facts whether *R* and *E* are located on identical loci of homologous chromosomes or are the dominants of two pairs of factors, each linked to the recessive allelomorph of the other.

6. It is shown that if the latter is the condition, crossing-over might occasionally occur between *R* and *E* with small likelihood of detection.² If crossing-over does occur, *RE* gametes are possible, which appears in turn to make possible true-breeding blues.

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² In ordinary practice poultry breeders make what are known as "pen matings," that is, one male is mated to a number of females and the offspring from these females are not kept separate. The exact parentage of any individual is therefore known only with regard to its sire, since its dam might be any one of the females in the group. As the detection of crossing-over depends upon the results of individual matings, it would be practically impossible to discover it under these conditions.

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BIBLIOGRAPHY

American Poultry Association.

1910. *The American Standard of Perfection*. 331 pp. Pub. by Amer. Poultry Assoc.

Bateson, W., and Saunders, E. R.

1902. Reports to the Evolution Committee of the Royal Society, I, 160 pp.

Bateson, W., and Punnett, R. C.

1905. Reports to the Evolution Committee of the Royal Society, II, pp. 99-131.

1906. Reports to the Evolution Committee of the Royal Society, III, pp. 11-23.

Baur, E.

1914. Einführung in die experimentelle Vererbungslehre. 2. neubearbeitete Auflage. viii + 401 pp. Berlin: Gebrüder Borntraeger.

Cole, L. J.

1914. Studies on Inheritance in Pigeons: I. Hereditary Relations of the Principal Colors. R. I. Agr. Expt. Sta., Bull. 158, pp. 311-380, pls. 1-4.

Goldschmidt, R.

1913. Einführung in die Vererbungswissenschaft. Zweite Auflage, xii + 546 pp. Leipzig: W. Engelmann.

Goodale, H. D.

1917. Crossing-over in the Sex Chromosome of the Male Fowl. *Science*, N. S., Vol. 46, No. 1183, p. 213.

Hagedoorn, A. L., and A. C.

1914. Studies on Variation and Selection. *Zeitsch. f. Ind. Abstamm. u. Vererbungslehre*, Vol. 11, No. 3, pp. 145-183.

Lloyd-Jones, O.

1915. Studies on Inheritance in Pigeons: II. A Microscopical and Chemical Study of the Feather Pigments. *Jour. Exp. Zool.*, Vol. 18, No. 3, pp. 453-495, pls. 1-7.

Nabours, R. K.

1914. Studies of Inheritance and Evolution in Orthoptera I. *Jour. Genet.*, Vol. 3, No. 3, pp. 141-170.

Pearl, R.

1917. The Probable Error of a Mendelian Class Frequency. *AMERICAN NATURALIST*, Vol. 51, No. 603, pp. 144-156.

Platt, F. L.

1916. "Western Notes and Comment." *Reliable Poultry Journal*, Vol. 23, p. 665.

Punnett, R. C.